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Opinion Article

# The Quest for Cognition in Plant Neurobiology

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## INTRODUCTION

Plant neurobiology[1] has emerged in the last few years as a result of the incorporation of new knowledge from well established areas of research such as plant electrophysiology, cell biology, molecular biology, and ecology. The difference between plant neurobiology and other more basic disciplines resides in the target of these interdisciplinary efforts which is the study of the complex patterns of behavior of plants qua information-processing systems.[i] Despite the youth of plant neurobiology, a body of empirical literature has grown and new results and questions have been reported and formulated.[2-3] Very recently, however, a number of researchers sceptical of the overall effort that plant neurobiology represents have teamed up in order to manifest their concern "with the rationale behind" the approach.[4] In their view, the newly born discipline does not furnish plant sciences, writ large, with any deeper understanding that is not in principle empirically achievable by, say, plant physiology.

This unnecessary tension between "lower" and "higher" level disciplines is not new to science. In the cognitive sciences, to take a close example, the neuron doctrine (for a review see ref. 5) claims that cognitive activity can be accounted for exclusively by basic neuroscience. Neuronal structure and function, as identified by neurophysiology, neuroanatomy and neurochemistry, furnish us with all we need to appraise the animal mind/brain complex. This approach ignores the integration of basic neuroscience with the rest of the cognitive science disciplines (psychology, linguistics, anthropology, artificial intelligence, and philosophy), an integration that has proved crucial to the understanding of the behavior of animals qua information-processing systems.[6] In view of Alpi et al.'s commentary, we run the risk of importing the aforementioned tension into the plant sciences literature. In general, the problem with reductionist approaches is the failure to recognize that the lower-level branches, conceptually speaking, only make sense in a higher-level (tissue, organ, system, social, etc.) context. In this sense, plant neurobiology differs from plant physiology[7] in the same way that cognitive neuroscience[8] differs from neurophysiology.

In addition, Alpi et al. target a straw man by interpreting plant neurobiology as suggesting that "higher plants have nerves, synapses, the equivalent of a brain localized somewhere in the roots, and an intelligence" (ref. 4, p. 135). And they continue, "there is no evidence for structures such as neurons, synapses or a brain in plants" (p. 136). In particular, Alpi et al. assume on behalf of plant neurobiologists the equation of auxin transport in plant cells with neuronal networks in animals. I do not wish to enter this empirical debate, although see Refs. 9 and 10 for rejoinders. In what follows I shall rather focus upon a conceptual misunderstanding that underlies Alpi et al.'s line of argument, and whose resolution will hopefully allow us to view the controversial topic of plant intelligence under a different lens.

## PLANT INTELLIGENCE AND THE DECENTRALIZATION OF COGNITION

In a series of exchanges,[11-13] Trewavas and Firn critically assess the concept of plant intelligence. Trewavas considers the concepts of learning and memory as applied to plants. Firn, in response, calls into question the very concept of a plant as an individual whose

[i]A general introduction to plant neurobiology can be found in http://131.220.103.188/ahlavacka/spn/society/index.php.

alleged intelligence is in dispute. Whereas animals grow and develop by means of alterations that affect the individual as such, plants grow and develop in terms of what Trewavas dubs "democratic confederations". In the latter case, there's no central processor ('cognizer')[iii] since growth and development don't operate upon the individual, but rather upon members or parts that may in fact be removed as the plant grows. As Firn points out, "any 'intelligence' that might be ascribed to 'the plant' could only reside in organs, tissues or cells because the concept of the plant as an individual is a misleading one" (p. 346). I agree with Firn that the concept of a plant as an individual is misleading, but not for the reasons he hints at in his reply to Trewavas. In fact, the concepts of both plants and animals as individuals are in my view equally misleading. The reasons for this are twofold.

On the one hand, when a cognitive scientist looks at the neural architecture that gives rise to animal cognition, he/she finds the same sort of problems that Firn identifies with regard to plants. As animals grow and develop attention is paid to many different processes at layers of organization that range from the subcellular level to the level of tissues and organs.[15-16] Biologically plausible forms of learning, such as Hebbian learning,[17] exploit correlated neural activity among neighbouring processing units. Learning thus consists in the local adjustment of synaptic patterns of connectivity. Likewise, the activation values of individual units depend exclusively upon the weighted values of those units that feed input into them. In this way, no individual as such shows up in the cognitive equation that accounts for memory and learning. Causal efficacy operates at levels below the level of the individual in such a way that no self is subject of scientific research unless broken down into its microconstituents and their interactions. In fact, we may say that the only self that exists is the phenomenal one that arises in conscious experience.[18] In short, it is the interactions that take place among processing units where the emergence of intelligence or cognition resides. This however has not prevented us from talking about cognitive capacities in the case of animals.

But the concept of an individual is equally misleading for a second related reason. Whereas according to the aforementioned considerations, we don't look at the level of the individual but rather at the level of its constituents, in a different sense, we ignore the level of the individual in favour of the level of an extended individual or an individual-coupled-with-its-environment. In the last few decades a number of positions which I shall refer to collectively as 'embodied cognitive science'[19-20] have exploited these insights, calling into question the concept of an individual as the (exclusive) seat of intelligence. The underlying idea is that in order to account for an agent's behavior we must treat it scientifically on a par with the environment in which the system is acting. In this way, an embodied cognitive science rejects the metaphor of cognition as a centralized process. Cognition is rather an emergent and extended self-organizing phenomenon whose explanation requires the simultaneous scientific understanding of neural, body and environmental factors as they interact with each other in real time.

In fact, it has become somewhat inescapable to accept that a final understanding of human intelligence will be embodied and embedded.[21] If embodied cognitive science is on the right track, the fact that the sort of highly sophisticated signal-integration behavior that we find in plants[22] happens to be 'decentralised' does not tell against the capacities of plants as such. Plants integrate in real time the information that is simultaneously provided by many different sensors on a variety of parameters, such as humidity, light or gravity, and many more.[23] From this perspective, plants and animals, as open systems coupled with their environments, are on a par. The target is the scientific understanding of the continuous interplay of both animals and plants in relation to the environmental contingencies that impinge upon them.

## THE QUEST FOR COGNITION

The debate on 'plant intelligence' is unfortunately plagued with conceptual traps.[iv] Intelligence is usually cashed out in animal or anthropocentric terms, in such a way that plants plainly fail to meet the conditions for animal or human-like intelligence, for obvious but uninteresting reasons. Nevertheless, in the name of scientific progress fight over labels ought to be avoided altogether. Plant neurobiology is not searching for the sort of tissues that implement computations in animals.[11] It goes without saying that plants do not share "neurons" with animals, or exhibit animal "intelligence". If the reader wishes to keep those terms for animals exclusively, so be it. Plant neurobiology interprets plants as information-processing networks with individual cells as computational building blocks. The emphasis is laid upon the computational functional profile[25] that accounts for the overt behavior of plants. The advantage is that from a computational point of view, we can abstract over implementation details in order to appraise the key features of plants as information-processing systems. This way, instead of asking whether plants can exhibit intelligent behavior, the question I wish to raise is: Do plants and animals compute, and if so, how can we understand their highly sophisticated adaptive responses? The debate framed in terms of "computations" may be less biased by inertias that relate to "intelligence", hopefully allowing us to bypass some of the aforementioned difficulties.

Put bluntly, an information-processing system counts as computational insofar as its state-transitions can be accounted for in terms of manipulations on representations. The relation of representation refers to the standing in of internal states of a physical system for the content of other states. Cognitive activity is thus marked by the processing of representational states. We need nonetheless a more stringent definition of 'representation'; a principled way to decide when a system manipulates representational states, beyond the somewhat trivial observation that one internal state 'stands in' for the content of another state. For present purposes, I propose to consider the following two principles.[26] First, according to a principle of dissociation, for a physical state to become representational, the state must be able on occasions to stand for things or events that are temporarily unavailable. And second, according to a principle of reification, a system state can only count as representational if it can be detected and a parallel drawn between the state in question

[iii]Someone may wish to deny the relevancy of the terms 'cognizer' and 'cognition' to plant neurobiology or plant behaviour, as these sciences are presently understood, unless the discussion is based on the deployment of metaphor. However, for present purposes, the sense in which plants may be said to 'cognize' is meant to be interpreted literally, in pretty much the same way that the cognitive architecture of insects has been the subject of empirical investigation.[14] In what follows I shall then consider plant behaviour from a cognitive perspective, granting realism to be the default theoretical stance, insofar as plants process information flexibly and adaptively.

[iv]Reference 24 is a good entry point to appraise how far we are from reaching an agreement on 'intelligence'.

and the role it plays in the establishment of a connection between the system's input and output states. That is, we must be able to identify specific physical states with the computational roles they are supposed to play.

This framework can serve to assess the cognitive capacities of any information-processing system whatsoever. Notice that it does not rely upon the existence of any specific brain tissue to perform computations. A physical state is contentful if it can be spatiotemporarily identified as causally efficacious in the connection of the system's input and output states in such a way that the state in question 'hangs in there' while the input state it is tuned to decays or is no longer present.[v] That's all that is needed. No restrictions in terms of implementation, neuronal or what may, are imposed. I propose therefore to adopt these two principles, taken together, as a condition on the possession of a cognitive architecture, and consider plants as candidates for its satisfaction.

## ON BEING SIMPLE MINDED[vi]

The capacities of plants are not only underestimated by (some) plant scientists. The philosophical literature is filled with examples that underestimate it too. Refs. 27-31 mention plants as the prototype of reactive behavior against which to contrast animal cognition. In fact, in relation to a constraint similar to the principle of dissociation in terms of spatiotemporal unbinding offered here, Haugeland considers a hypothetical "super-sunflower". Whereas a sunflower requires continuous stimulation to be processed in a reactive manner, a super-sunflower can perform solar-tracking by representing internally the trajectory of the sun as it moves. The purpose of the example is precisely to mark the watershed between plant reactive behavior from animal cognitive one (super-sunflowers would fall within the cognitive side of the spectrum). But, super-sunflowers are only a thought experiment. Plants are thought to be reactive insofar as their behavior is said to be automatic; remaining invariant under a variety of conditions. This however only reflects our ignorance of what plants can do (for a review see ref. 11).

Curiously enough, the philosophical literature is not as sceptical with respect to insects as it is with regard to plants. According to Carruthers ants and bees have minds. In the case of bees, Carruthers mentions that "bees can learn the expected position of the sun in the sky at any given time of day, as measured by an internal clock of some sort" (ref. 31, p. 213). These complex behavioral patterns are clearly not merely reactive responses. In fact, ref. 34 studied the way bees and a number of other insects estimate the sun's position in the absence of daylight. It is not clear what the computational mechanisms involved are but the working hypothesis seems to be that bees "can generate an internal representation that incorporates spatial and temporal features of the sun's course that they have never directly seen" (p. 4471). Whatever the mechanism is, it cannot be associative since learning involves the manipulation of internal information in the absence of direct solar stimulation (principle of dissociation, above).

Are we then surrounded by "super-bees" and "dumb-plants"? Do they fall on the cognitive and reactive sides of the spectrum, respectively? I don't think so. Plants do model environmental regularities in order to predict the future. Off-line nocturnal reorientation by plant leaves, for example, represents a qualitative change with regard to more reactive behavior.[vii] Leaf laminas of *Lavatera cretica* can, not only anticipate the direction of the sunrise, but also allow for this anticipatory behavior to be retained for a number of days in the absence of solar-tracking.[36] That is, the laminas reorient during the night and keep facing the direction of the sunrise even after a few days without tracking the sun, and without sensing the position of sunset. Schwartz and Koller showed this behavior to constitute a complex off-line response. The nocturnal reorientation behavior exhibited by some exemplars lasted for as long as 3–4 days in the absence of daytime solar-tracking. Such a modelling behavior is a stepping stone that distances plant off-line computational capabilities from merely reactive ones.

The explanation of the sun-tracking behavior in the absence of daylight in some plants involves the internal modelling of environmental rhythms. Circadian clocks allow for time-estimation by synchronizing endogenously generated activity with exogenous cyclic periods such as day-night planetary patterns, mimicking biological rhythms on a 24-hour cycle. This explains nocturnal reorientation in the absence of sunrise stimulation. The case of nocturnal reorientation in plants is thus not that different from the bees' example. Plant genetics points towards underlying shared molecular components that explain day-length estimations and the operation of light receptors. In the case of time-estimation, recent research in genomics has unearthed the molecular mechanisms, with the striking result that both plants and animals draw on the very same molecular networks in their adaptive exploitation of circadian clocks.[37]

What unites animals and plants in evolutionary terms is the need to exploit an internal memory that allows organisms to remodel their behavior in order to optimize fitness. That points towards shared forms of memory and learning. Once we stick to the molecular level, things don't look that different across the eukaryotic kingdom. An inference to the best explanation would point towards a rather ancient starting point in the configuration of such mechanisms. Time-estimation gives rise to a primitive form of anticipatory behavior that has proven critical in phylogenesis. Nervous systems in animals then diverged at some point in the evolutionary trajectory, due to different pressures and needs from those of sessile plants.[11] However, this divergence is neutral with regard to the capacities exhibited from a computational point of view. Nothing then prevents other information-processing systems from possessing minds.

## CONCLUSION

Do plants compute? The blunt answer is "yes". Plants compute insofar as they manipulate representational states. The *sine qua non*

[v]Incidentally, Trewavas (ref. 11) notes that "[ref. 32] regarded the early expressions of intelligence in animals as resulting from delays in the transfer of information between the sensory system and the motor tissues acting upon the signals. The delay enabled assessment of the information and modification of information in the light of prior experience, and it was that assessment that formed the basis of intelligence." The reader can see how nicely these comments fit with the framework advocated here.

[vi]The title of this section is somewhat ironically borrowed from reference 31. According to ref. 31 ants and bees, but not plants, possess minds in the relevant cognitive sense. In ref. 33 I propose to pave the way for a reductio against Carruthers' polemic view. In particular, I argue that if ants and bees have minds, by the same token, plants do have minds too. As will become apparent in this section, the reductio need not be virtueless. I'm indeed happy to accept that both insects and plants are cognitive creatures.

[vii]Reference 35 elaborates further the material of this section.

[viii]See for example reference 38 for a review of data that points to the interaction of circadian clocks with hormones and light patterns.

of representation-based competency is off-line adaptive behavior.[21] Reactive behavior differs from truly cognitive one because it fails to meet the principle of dissociation (the states of a reactive system covary continuously with external states). Off-line competencies thus mark the borderline between reactive, noncognitive, cases of covariation and the cognitive case of intentional systems. Nocturnal reorientation in *Lavatera cretica* leaves is not to be interpreted in reactive terms, since such a competency is not explained by means of online forms of covariation.

For purposes of illustration I chose a case, nocturnal reorientation, where the principle of dissociation is clearly met. But, as we saw, there is a further 'principle of reification' whose satisfaction would involve the identification of specific physical states with the roles they play. In relation to this principle of reification, it could be the case that the system is not subject to de-composition, failing thus to meet the principle and therefore to exhibit genuine cognition. The acknowledgement of this possibility could be due to the fact that the internal states of the system are massively and reciprocally causally connected.[26] This, however, only represents a challenge that plant neurobiology would be willing to take on: Namely, the challenge of identifying and assigning representational roles to the sub-states and processes that plant neurobiology eventually discovers in the future. Or to put it another way, this possibility simply tells against the accomplishments of today's best plant science theories.

Alpi et al. "urge the proponents of plant neurobiology to reevaluate critically the concept and to develop an intellectually rigorous foundation for it" (ref. 4, p. 136). In this review we've seen that questions can be structured in a different way. In section 2 we saw that an embodied cognitive science requires the simultaneous scientific understanding of neural, body and environmental factors as they interact with each other in real time. The ability of plant leaves to track the sun is not only a case of cognitive, nonreactive covariation, but also a case where cognition decentralizes. Successful tracking behavior requires the manipulation of information which is continually updated and combined with endogenous data. Embodied cognition lays the stress upon real-world situations as the context in which cognition takes place and makes sense.[viii] Other "cognitive" abilities such as flowering years ahead of time, computing the location of shade ahead of time by sensing reflected far-red/red light, synchronizing growth patterns with periods when water will be available (see ref. 22 for a review of these and other predictive powers) must be studied in the light of an embodied cognitive science. Plant neurobiology must unearth all the real, not hypothetical, "super-sunflowers" around us, spelling out the sense in which plants are embodied. Plant neurobiology confronts the same sort of questions with respect to plant physiology that cognitive neuroscience does in relation to basic neuroscience. Its target is the explanation of the mechanisms that underlie signalling as plants interact in real time in complex environments and adapt phenotypically to them.

Seeing 'plant neurobiology' as a catch-phrase only shows that the connection between basic and cognitive neuroscience has not arrived to the plant sciences literature, and needs to be spelled out. The neurocomputational features of plants are meant to be taken literally. If we are to discuss the capacities of living organisms, the aim is to assess the computational capabilities of eukaryotes generally speaking. In short, we want to know how far a full-blown embodied cognitive science can go in the integration of eukaryote life forms. As more knowledge is gathered in areas such as "genomics and bioinformatics" (see ref. 1 and references therein), a better understanding will be obtained of how molecular and cellular networks relate to overt behavior at the *plant-coupled-with-its-environment* level. That is the arena in which an integrated plant neurobiology ought to be founded and critically assessed.

**References**


1. Brenner ED, Stahlberg R, Mancuso S, Vivanco J, Baluška F, Van Volkenburgh E. Plant neurobiology: An integrated view of plant signalling. Trends Plant Sci 2006; 11:413-19.
2. Baluška F, Mancuso S, Volkmann D. Communication in plants: Neuronal aspects of plant life. Berlin: Springer-Verlag, 2006.
3. Barlow PW. The minimum number of cells required to innervate the root brain of plants. BioEssays; Submitted.
4. Alpi A, Amrhein N, Bertl A, Blatt MR, Blumwald E, Cervone F, Dainty J, De Michelis MI, Epstein E, Galston AW, Goldsmith MH, Hawes C, Hell R, Hetherington A, Hofte H, Juergens G, Leaver CJ, Moroni A, Murphy A, Oparka K, Perata P, Quader H, Rausch T, Ritzenthaler C, Rivetta A, Robinson DG, Sanders D, Scheres B, Schumacher K, Sentenac H, Slayman CL, Soave C, Somerville C, Taiz L, Thiel G, Wagner R. Plant neurobiology: No brain, no gain? Trends Plant Sci 2007; 12:135-6.
5. Gold I, Stoljar D. A neuron doctrine in the philosophy of neuroscience. Beh Brain Sci 1999; 22:585-642.
6. In: Wilson RA, Keil FC, eds. The MIT Encyclopedia of the Cognitive Sciences. Cambridge, MA: MIT Press, 1999.
7. Taiz L, Zeiger E. Plant Physiology. New York: Sinauer, 2002.
8. Gazzaniga M, Ivry R, Mangun G. Cognitive neuroscience: The biology of the mind. New York: Norton, 2002.
9. Trewavas AJ. Plant neurobiology: All metaphors have value. Trends Plant Sci 2007; 12:231-3.
10. Brenner ED, Stahlberg R, Mancuso S, Baluška F, Van Volkenburgh E. Plant Neurobiology: The gain is more than the name. Trends Plant Sci; In press.
11. Trewavas AJ. Aspects of plant intelligence. Ann Bot 2003; 92:1-20.
12. Trewavas AJ. Aspects of plant intelligence: An answer to Firn. Ann Bot 2004; 93:353-7.
13. Firn R. Plant intelligence: An alternative point of view. Ann Bot 2004; 93:345-51.
14. Menzel R, Giurfa M. Cognitive architecture of a mini-brain: The honeybee. Trends Cog Sci 2001; 5:62-71.
15. Churchland PS, Sejnowski TJ. The computational brain. Cambridge, MA: MIT Press, 1992.
16. Elman JL, Bates EA, Johnson MH, Karmiloff-Smith A, Parisi D, Plunkett K. Rethinking innateness. Cambridge, MA: MIT Press, 1996.
17. Rolls ET, Treves A. Neural networks and brain function. Oxford: Oxford University Press, 1998.
18. Metzinger T. Being No One. Cambridge, MA: MIT Press, 2003.
19. Núñez R, Freeman WJ. Reclaiming Cognition. Thorverton UK: Imprint Academic, 1999.
20. Pfeifer R, Scheier C. Understanding Intelligence. Cambridge, MA: MIT Press, 1999.
21. Clark A. Being there: Putting brain, body and world together again. Cambridge, MA: MIT Press, 1997.
22. Trewavas AJ. Green plants as intelligent organisms. Trends Plant Sci 2005; 10:413-9.
23. Baluška F, Barlow PW, Volkmann D, Mancuso S. Gravity related paradoxes in plants: Plant neurobiology provides the means for their resolution. In: Witzany G, ed. Biosemiotics in Transdisciplinary Context: Proceedings of the Gathering in Biosemiotics 6. Umweb: Helsinky, 2007.
24. Schull J. Are species intelligent? Beh Brain Sci 1990; 13:68-113.
25. Polger T. Computational Functionalism. In: Symons J, Calvo F, eds. The Routledge Companion to Philosophy of Psychology. Oxford: Routledge, (forthcoming).
26. Calvo Garzón F. Towards a general theory of antirepresentationalism. Brit J Phil Sci; In press a.
27. Haugeland J. Representational genera. In: Ramsey W, Stich S, Rumelhart DE, eds. Philosophy and connectionist theory. Hillsdale, NJ: Lawrence Erlbaum Associates, 1991.
28. Cantwell Smith B. On the origins of objects. Cambridge, MA: MIT Press, 1996.
29. Tye M. The problem of simple minds: Is there anything it is like to be a honey bee? Philosophical Studies 1997; 88:289-317.
30. Clark A. An embodied cognitive science? Trends Cog Sci 1999; 3:345-51.
31. Carruthers P. On being simple minded. American Philosophical Quarterly 2004; 41:205-20.
32. Stenhouse D. The Evolution of intelligence-a general theory and some of its implications. London: George Allen and Unwin, 1974.
33. Calvo Garzón F. On the cognitive architecture of insects and other information-processing systems: Reply to Carruthers; Submitted.
34. Dyer FC, Dickinson JA. Development of sun compensation by honeybees: How partially experienced bee estimate the sun's course. Proc Natl Acad Sci USA 1994; 91:4471-4.
35. Calvo Garzón F. Plant neurobiology: Lessons for the Unity of Science. In: Rahman S, Symons J, Torres M, Pombo O, eds. The unity of science: Essays in honour of Otto Neurath. Dordrecht: Kluwer; In press b.
36. Schwartz A, Koller D. Diurnal phototropism in solar tracking leaves of Lavatera cretica. Plant Phys 1986; 80:778-81.
37. Cashmore AR. Cryptochromes: Enabling plants and animals to determine circadian time. Cell 2003; 114:537-543.
38. Nozue K, Maloof JN. Diurnal regulation of plant growth. Plant Cell Envi 2006; 29:396-408.